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Abstract

Sudden death syndrome (SDS) caused by *Fusarium virguliforme* is one of the major yield-limiting soil borne diseases of soybean (*Glycine max*). The SDS has been reported from 21 U.S. states and is known to occur in Africa, North America, and South America. In the U.S. the losses due to SDS was estimated at $3.06 billion for a period from 1988 to 2010. Since 1983, several management approaches have been investigated to reduce SDS and yet, continued efforts are necessary to develop long term disease management programs and to sustain disease below economic threshold levels. Integrating available control measures is an option, but adaptability and real-world assessments are equally important. Support of several funding agencies to better understand the disease in identifying suitable control measures to reduce yield losses in commercial cultivations has been indispensable in accomplishing these goals. In spite of sustained efforts, SDS continued to spread within the U.S. and reported in seven other countries since its first report in 1971. Comprehensive reviews have previously been published on this disease by Roy *et al.* [98], Leandro *et al.* [58], and Hartman *et al.* [32]. In this review, updated information on geographic distribution and economic significance of SDS, epidemiology, factors affecting SDS, and management options for SDS including screening techniques have been compiled. Also, discussed significant gaps in use of plant, fungi and bacteria based biocontrol agents in addressing management of SDS.

Keywords: Soybean sudden death syndrome, SDS, *Fusarium virguliforme*, biocontrol, global reports, yield losses due to SDS, epidemiological factors, greenhouse and field screening.

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Review methodology: The following keywords were used in different combinations in searches on google, google scholar and CAB direct; first report(s) of soybean sudden death syndrome; yield losses due to soybean SDS; historical soybean prices per bushel or metric ton; factors affecting soybean SDS; management of soybean SDS; greenhouse and field screening techniques for SDS; biocontrol of soybean SDS; fungicide seed treatments; bio-fertilizer; host range; *Fusarium brasiliense*; *F. crassistipitatum*; *F. solani* f. sp. *glycines*; *F. tucumaniae*, and *F. virguliforme*; interaction between cyst nematode or *Heterodera glycines* on soybean SDS; back references cited in published articles, graduate theses, and unpublished data of several authors.

An overview of soybean

Taxonomy of the *Glycine* spp., and domestication [45], origin, history, and uses of soybean [27, 45, 61], history and growth of soybean plants including germplasm collections, utilization, plant improvement, growth and development [44] have been well documented. Soybean [*Glycine max* (L.) Merr.] is the leading oilseed crop produced and consumed in the world with the crop grown in 70 countries with an annual production of 268 million metric tons (mmt). Average world soybean production has increased from 115 mmt in 1993 to 308 mmt in 2014 and soybean prices (USD/ton) in top five producers (Argentina, Brazil, China mainland, India, and United States) fluctuated significantly between 1993 and 2014 [24]. According to Hymowitz *et al*. [44] top producers of soybean are the United States (31% of the world's total), Brazil (31%), Argentina (19%), China (5%), India (4%), Paraguay (3%) and Canada (2%). As of August 2016, USDA global production analysis projection of 2016/2017 world soybean production was 330.41 mmt, an increase of 17.74 mmt or a 5.67% compared with previous year [pecad.fas.usda.gov]. According to USDA Agricultural Projections to 2025, world trade is projected to increase in soybeans by 22%, soybean meal by 20%, and soybean oil by 30% [ers.usda.gov].

Global occurrence of sudden death syndrome

More than 200 plant pathogens affect soybean worldwide, of which at least 35 have been reported economically important [37]. Details of diseases in some of the major soybean producer countries such as Argentina, Brazil, Canada, China, India, Japan, and the United States have been compiled

by Hartman *et al*. [36]. Sudden death syndrome of soybean, caused by an Ascomycete fungus *Fusarium virguliforme* O'Donnell & T. Aoki in North America [7], and South Africa [125], *F. brasiliense* T. Aoki & O'Donnell, *F. crassistipitatum* Scandiani *et al*., *F. cuneirostrum* O'Donnell & T. Aoki, *F. tucumaniae* T. Aoki *et al*., and *F. virguliforme*, in South America [6–8, 90] is an economically significant soil-borne disease, and a risk to many soybean production areas worldwide. The disease was first observed by H.J. Walters in Arkansas, United States in 1971 [100], but it was only in 1983 that the disease was named as sudden death syndrome (SDS) of unknown etiology [40]. As of this review, the disease has been reported in three continents, North America (Canada and United States), South America (Argentina, Bolivia, Brazil, Paraguay, and Uruguay), and Africa (South Africa), and within the United States 21 states (Fig. 1). Also, *F. virguliforme* was isolated from soil in Malaysia [16], however, occurrence of SDS on soybean is yet to be recorded in that country. Similarly, *F. solani* f. sp. *glycines* has been reported in India not as SDS-causing pathogen but as a soybean wilt causing pathogen [Personal communication with Drs. Shamarao Jahagirdar, AICRP on Soybean, University of Agricultural Sciences, Dharwad, Karnataka, India, July 2016 and Rajesh K. Varma, ICAR-Indian Institute of Soybean Research, Indore, Madhya Pradesh, India, July 2016]. Also, in Japan, *F. azukicola* T. Aoki, Suga, F. Tanaka, Scandiani & O'Donnell, was able to induce root rot and typical SDS symptoms in soybean [9]. Whether the pathogens causing SDS have been introduced in to new regions or if they have been present in the soil in production fields of these countries for some time without being detected is unknown. After the SDS was detected in Iowa [150], Scherm and Yang [114] developed a risk assessment model to determine potential geographic range of development of this disease, which was considered a southern disease by then, in North America. They predicted potential northward development of SDS and cooler production regions in the North Central United States to have higher risk than southern soybean production regions. Eighteen years after their publication, occurrence and distribution of SDS confirmed accuracy of their predictions [114]. Future reports of SDS in India, Japan and Malaysia on soybeans would be an interesting development of this disease.

Economic significance of SDS

Historic yield losses due to SDS in the United States compiled from various sources [21, 35, 53, 96, 116, 132–134, 136–141] ranged from 0.06 mmt in 1988 to 1.91 mmt in 2010 with the highest yield loss of 2.10 mmt recorded in 2000. The corresponding economic losses due to SDS varied from $15.7 million in 1988 to $669.2 million in 2010 (Fig. 2). The economic losses were based on NASS-USDA soybean prices at $7.5/bushel ($275.6/metric ton) in 1988 and $9.6/bushel ($352.7/metric ton) in 2010 (Fig. 2). Though the estimated yield loss of 2.10 mmt in 2000 was highest compared to yield loss of 1.91 mmt in 2010, due to differences in soybean prices the economic loss in 2000 was $342.7 million ($4.5/bushel or $163.5/metric ton), which is almost half the economic loss recorded in 2010 at $669.2 million. On the contrary, the soybean prices in 2008 were highest ($385.1/metric ton) compared with other years between 1988 and 2010, the economic loss was estimated at $209.6 million due to less yield losses of only 0.54 mmt in 2008. An estimated average yield loss due to SDS from 1988 to 2010 was 0.56 mmt (range 0.03–2.10 mmt) and corresponding average economic loss was $133.3 million (range $8.1–669.2 million) at an average soybean price at $233.24/metric ton (range $152.5–385.1/metric ton). Yield losses due to SDS vary widely depending on planting dates [39, 123, 135], maturity groups, cultivar selection [123], climatic and environmental trends during the growing season [57], glyphosate spray and many more dynamics as outlined in factors affecting SDS. Also, economic losses vary depending on the market price of soybean in a given year and primary factors affecting the market price according to USDA Economic Research Service include, population and income growth, demand for livestock products, as well as export import policies. In this review, the yield and economic losses due to SDS in Canada, South American countries and South Africa were not calculated because of non-availability of historical data.

Symptoms of SDS

Soybean plants infected with SDS show symptoms both during seedling (Fig. 3A-E) and the most dramatic symptoms in reproductive growth stages (Fig. 3F-K) similar to Roy *et al.* [98]. Characteristic symptoms include, appearance of small yellow flecks or chlorotic spots that coalesce to cause interveinal chlorosis. As the disease progresses, interveinal chlorosis turns into interveinal necrosis and the affected leaves twist and curl giving puckering and mottling appearance that defoliate prematurely with leaf petiole remaining intact on the stem. Flowers and

pods abort and developing pods may not entirely fill. Symptomatic plants exhibit blue-stained fungal sporodochia on taproot (Fig. 3K). Factors that favor symptom development are cool, moist conditions early in the growing season leading to higher disease incidence. Also, early planting, high rainfall and/or low-lying, poorly drained or compacted areas of the fields other important factors that lead to higher incidence. Above-ground symptoms are caused mainly by a toxin produced by the fungus and translocated through the plant. The disease severity varies from field to field depending on the above conditions and field history.

Infection process and survival of *F. virguliforme*

The occurrence of *F. virguliforme* infection early in the season is the result of colonization in xylem tissue, which provides a pathway for upward movement of phytotoxin that are essential for foliar symptom expression [83, 86] and lignin degradation by *F. virguliforme* may play an important role in the infection, colonization, and survival of the fungus in the root tissue [62, 63]. Navi and Yang [83] reported that, plants with SDS foliar symptoms showed both external and internal discolored taproots and basal stems, while plants with no foliar symptoms had only superficial external discoloration. Microtome sectioning of taproots of symptomatic plants revealed the presence of fungal structures in both xylem and phloem tissues, while plants with no foliar symptoms revealed fungal structures only in phloem tissue. Based on their findings Navi and Yang [83] suggested an effective and ineffective colonization zones of the fungus for symptomatic and asymptomatic plants, respectively (Fig. 4).

The SDS fungus survives between crops in soil and crop residue (corn and soybean) either as conidia or chlamydospore [84, 98], on decomposed soybean roots post-harvest [100, 101], inside soybean cyst nematode [67, 68] and in no-till fields [71, 100]. This pathogen can also reproduce on corn, wheat, ryegrass, pigweed, sugar beet, lambsquarters, canola, alfalfa, pinto bean, navy bean, white clover, red clover, pea, and Canadian milk vetch without causing symptoms on these hosts [55]. Researchers have been puzzled by the fact that SDS has now become more prevalent in the Corn Belt and there were many observations that severe SDS occurred after continuous corn. Recently, Navi and Yang [84] investigated effects of rotation with corn on *F. virguliforme* survival. Their results showed that corn residue, particularly coarse-ground corn kernels, harbor *F. virguliforme* significantly in the absence of soybeans. Also, studies conducted

by Abdelsamad *et al*. [1] with a 2-year rotation of corn and soybean showed greater SDS incidence and severity, and lower yield, compared to the 3-year corn-soybean-oat/red clover, and 4-year corn-soybean- oat/alfalfa-alfalfa rotations. Thus *F. virguliforme* remains a growing threat to global soybean production.

Factors affecting occurrence of SDS

There are numerous factors that affect SDS such as; effects of herbicides on metabolic activities and growth of host and pathogens and increase in soil-borne diseases as a result of herbicide-pathogen interaction [3], interaction between *F. virguliforme* and cyst nematodes [26, 99, 103, 143, 144], biotic and abiotic factors [98], irrigation and cyst nematodes [70], irrigation and soil compaction [20], tillage [117, 127, 128, 135], inoculum density [28], isolates and inoculum rate [31], genetic structure and variation in aggressiveness of *F. virguliforme* [66], soil variables including fertility parameters [105, 112], soil temperature [29, 113], water matric potential in soil [113], relation of sand content, soil pH, and soil nutrients [109], cultivars [39, 89, 101, 105, 127, 135], genetic architecture of soybean [156], planting date [39, 52, 135], crop rotation and crop sequences [93, 104, 142], root system [91], plant age [29, 30], early infection and xylem colonization [83, 86, 154], biochemical response of soybean roots [62], toxin production by pathogen [12], herbicides spray [22, 50, 77–79, 107, 108, 147], light [49], elevated atmospheric carbon dioxide and ozone [23], climatic and environmental trends [57], symptomatic and asymptomatic host-range [55], fungicide and cultivar interactions [51], and seed treatment and plant population [2, 52, 155].

Management options of SDS

The sudden occurrence and unpredictable nature of soybean SDS make the disease so far the most puzzling one to manage in soybean production. Development of the disease depends on several factors listed above. However, a number of approaches listed below either alone or by integration of several methods can help reduce SDS impact in commercial production. Management options of SDS to break the life cycle of the pathogen (Fig. 5) include delayed planting [39, 123, 135], planting SDS tolerant varieties [102, 108], fall tillage [135, 137], crop rotation [1, 104, 137, 142],

modifying agronomic practices like row spacing and seeding rate [123], fungicide seed treatments [52, 72, 82, 130, 131, 155], seed treatments with a combination of fungicides, systemic insecticides and biological(s) [2, 155], seed treatment with bacteria and fungi based biocontrol agents [43, 75, 87, 129], preplant or foliar applied potassium chloride with fungicides [88], cultural and biological control [4], exploring potential untapped resistance sources in perennial *Glycine* spp. to improve resistance in soybean [33] and recovering SDS infected plants [79] similar to sorghum and pearl millet [120, 121], plant resistance, variety selection, adjusting planting dates, crop rotation, seed treatment with bio-fungicide [149], identification of quantitative trait loci [145], genomic approaches to molecular breeding of resistance [46], integrated approaches [34], clean harvest of corn and soybean [84, 151] and genetic engineering along with other traditional management options may be needed as integrated approaches to manage SDS [32].

Recently, Navi and Yang [75] have summarized HeadsUp (a plant based biocontrol product) seed treatment or foliar spray studies of 11 years starting in 2005 covering six states in North Central regions of the United States. Results showed that HeadsUp has effectively suppressed SDS and white mold (*Sclerotinia sclerotiorum* (Lib.) de Bary) and improved an average yield of 0.142 mt/ha (range -0.830 to 1.095 mt/ha) compared with controls (Fig. 6). Compared with control, the proportions of yield response to treatments were 62% increase, 9% no change, and 29% decrease in 68 field trials. There is a slightly larger number of low responsive trials for HeadsUp compared with synthetic chemicals, which is often seen in field trials with biological control products. However, the low cost and environmental friendly make HeadsUp a good candidate for soybean disease management.

Resistance screening in greenhouse conditions

Several greenhouse methods for host resistant screening that are previously reported in the literature that have been successful in identifying soybean resistant to SDS. These include dip inoculation of sprouted seed in *F. virguliforme* spore suspension and planting in greenhouse mix [80, 81, 85], temperature-controlled water bath method [38], exposing cut stem to cell free culture filtrate [42], molecular marker-assisted breeding for resistance [60], toothpick inoculation and soil infestation methods [111], planting seeds in a mixture of 1 part inoculum with 20 part soil [64], using cones filled with steam-treated soil mix (2:1 sand: soil) and topped with 3 g of fungus

infested white sorghum grains [25]. Navi and Yang (unpublished), modified greenhouse screening technique [80, 81, 85] to identify resistance sources in germplasm and explore efficacy tests of seed treatments with biocontrol agents (BCA) and or chemicals against SDS (Fig. 7). The modified method of Navi and Yang [unpublished] in brief is as follows; White sorghum grains infested with *F. virguliforme* [84] were sprinkled into plastic tub containing potting mixture (two parts of steam-sterilized sand and one part black soil) at 1% of the potting mixture (Fig. 7A), and the inoculum was mixed with the potting mixture (Fig. 7B). White foam cups (237 ml, Dart Container of Michigan LLC, 500 Hogsback Rd., Mason, MI 48854) were filled-up with the mixture, and the planting spots were marked at equidistant (1.5-cm apart) and at uniform depth of 2-cm (Fig. 7C) with hand held wooden planter (Fig. 7D) fabricated at General Services workshop facility, Iowa State University. Placed 5-7 seeds (commercially untreated seeds that were treated with either BCA spore suspension or fungicide at 5 ml/kg of seed) in marked spots (Fig. 7E) and pressed the seed to uniform depth of 2-cm with the planter. The seed was covered with additional potting mixture and was compacted it (Fig. 7F) with hand held wooden compactor (Fig. 7G) and watered the cups to the saturation point. Cups were incubated on greenhouse benches in 16-h light under 400W E-Ballast, Metal Halide type M59 bulb, (120v/HPS/MH, Digital Sunburst, Hydrofarm Inc. 2249 S. McDowell Ext., Petaluma, CA, 94954). During the incubation, plants were watered twice daily. Two weeks after planting, stand count and initial SDS counts were recorded. Subsequently, 30 and 45 days after planting, SDS infected plants count and SDS plants showing production of symptomless leaves that previously had one or more unifoliate and or trifoliate leaves with SDS symptoms and their severities were recorded. Authors are using this method from 2010 till date to evaluate seed treatment industry protocols and in academic research.

Resistance screening in field conditions

Identifying resistance to SDS remains a major effort for soybean industry because variety selection is the most effective source for producers in SDS risk management. Resistance breeding has made progress over the past 20 years with a limited success due to the fact that SDS resistance is controlled by multiple genes, which makes resistance screening for a large number of entries difficult. Currently, selections and evaluations for resistance to SDS largely depends on both greenhouse and field evaluations. Every season, breeding lines are evaluated in fields either with

history of SDS or in fields inoculated with *F. virguliforme* fermented on oats a method initially developed by Yang *et al*. [148]. In this method, SDS incidence and severity increased with an increased ratio of oat to soybean seeds, reaching a maximum level at about 4:1. Subsequently, this method was modified in 2006 [20] for establishing field nurseries and in 2008 [Navi and Yang, unpublished] to assess efficacy of biological and chemical seed treatments or seed treatment plus foliar sprays. The modified method of Navi and Yang [unpublished] in brief is as follows; increased *F. virguliforme* on white sorghum grain [84], sampled separately a known number of soybean seed at 10 seed/linear foot (76.2-cm) in 8.5 × 20.3-cm envelops and the *F. virguliforme* fermented sorghum grain at 5cc/linear foot. The seeds of individual treatment and the inoculum were then placed into a cone plot planter (2- or 4-rows). Planted soybean seed along with the fermented sorghum grain using ALMACO 4-Row SeedPro Precision Vacuum planter with an automatic cable winding trip system. Applied post-emergence herbicide (if required) prior to setting up rainbird overhead sprinklers. Run the sprinklers on non-rainy days from vegetative growth stage-4 (four unfolded trifoliate leaves) to reproductive growth stage-6 (full seed setting) to provide either irrigation water or rainfall a total of 2.5 cm/week. Recorded stand count in vegetative growth stages at 15 and 30 days after planting and SDS plants count and severities both in vegetative (Fig. 3A-D) and reproductive growth stages (Fig. 3F-J) at regular intervals up to R8. This method has an increased consistency of SDS symptom expression across replications in testing efficacy of biological and chemical seed treatment products and or the foliar sprays against SDS and is extensively used by the authors to test industry protocols. Also, the method is in use to test advanced breeding lines with different maturity groups [19].

Conclusion and future research opportunities

Understanding the nature of sudden death of a soybean plant colonized by SDS fungus and occurrence of sudden blight of a soybean field due to SDS so far remained the major challenge in developing effective management measures. Development of a SDS resistance screening method which can handle a large number of entries in a short period of time remains one of the major challenges for SDS research. Currently, the seed treatment with ILeVo appears promising, although foliar symptoms do occur if the variety is susceptible to SDS. Information technology enabled us to study this disease using a non-traditional approach, which may provide new insight

on the sudden occurrence of this disease. Yang *et al*. [146] showed SDS to be a model system in the study of satellite remote sensing for disease detection. This is the first reported case of occurrence of a plant disease that can be seen and identified from satellite due to its unique nature.

Based on currently available literature search, several possible scenarios have been discussed to improve soybean SDS management. However, we have observed that there is a significant gap in the use of fungi or bacteria based biocontrol agents (BCA) in management of SDS. Therefore, much needed emphasis is essential on use of BCA that have strong mycoparasitism and antagonism characters. Also, BCA seed treatment with bioAPT [87] a microbial carrier powder (American Peat Technology, LLC, Aitkin, MN, U.S.A.) or without the carrier [43, 129], application of BCA along with pre-planting fertilizers and herbicides, and or foliar spray need to be standardized to have suitable synergism and compatibility. Although, *Fusarium* spp. causing SDS are not seed borne except one report [10], but seed treatments with BCA provide mycoparasitism potentials of the target pathogen in the vicinity of seed germination zone by which early infection and subsequent toxin production could be minimized. In addition, application of BCA in any of the arrangements stated above should have long term benefits as most fungi or bacteria based BCA increase their population much faster than the target pathogen on crop residue and if conditions are unfavorable they survive in soil and residue by producing chlamydospores. If the BCA has potential to mycoparasitize hyphae, conidia or chlamydospores of the target pathogen, it is predictable to have an added advantage.

The activity of BCA is mainly attributed to various anti-microbial/antagonistic compounds they produce [13, 15, 41], competition for nutrition and space [14, 59, 122], antibiosis [115], antagonism effects [71], and mycoparasitism capabilities [17, 48, 97]. Full exploitation of the BCA potential could provide growth enhancement of domestic plants, green house plants, and agricultural crops [65, 126]. Becker Underwood Inc. (now with BASF chemical company) has developed bacterium based HiStick N/T (currently Nodulator N/T) a peat-based inoculant and disease protection seed treatment product in soybean to suppress *Rhizoctonia* spp. and *Fusarium* spp. (BASF.com). Also, Organic Materials Review Institute (omri.org) has developed *Trichoderma* spp. based soil amendment and bio-fertilizer (Custom GP) to improve overall conditions of the soil aimed at healthier roots and stronger plant growth. Recently, a team led by scientist Aradhana Mishra, National Botanical Research Institute, one of the constituent research institutes of the Council of Scientific and Industrial Research, New Delhi, India developed

Trichoderma spp. based bio-fertilizer to mitigate greenhouse gases and to repair damaged root tissues of various agriculture crops, thereby increasing productivity (article appeared in Times of India, Indian National Newspaper, June 6, 2016). Wide-ranging commercial BCA registered under the United States Environmental Protection Agency, *Trichoderma* spp. based biofungicide agents and agriculture products [106, 126] and other commercially available biocontrol products used against several plant diseases [76] can be explored in management of soybean SDS.

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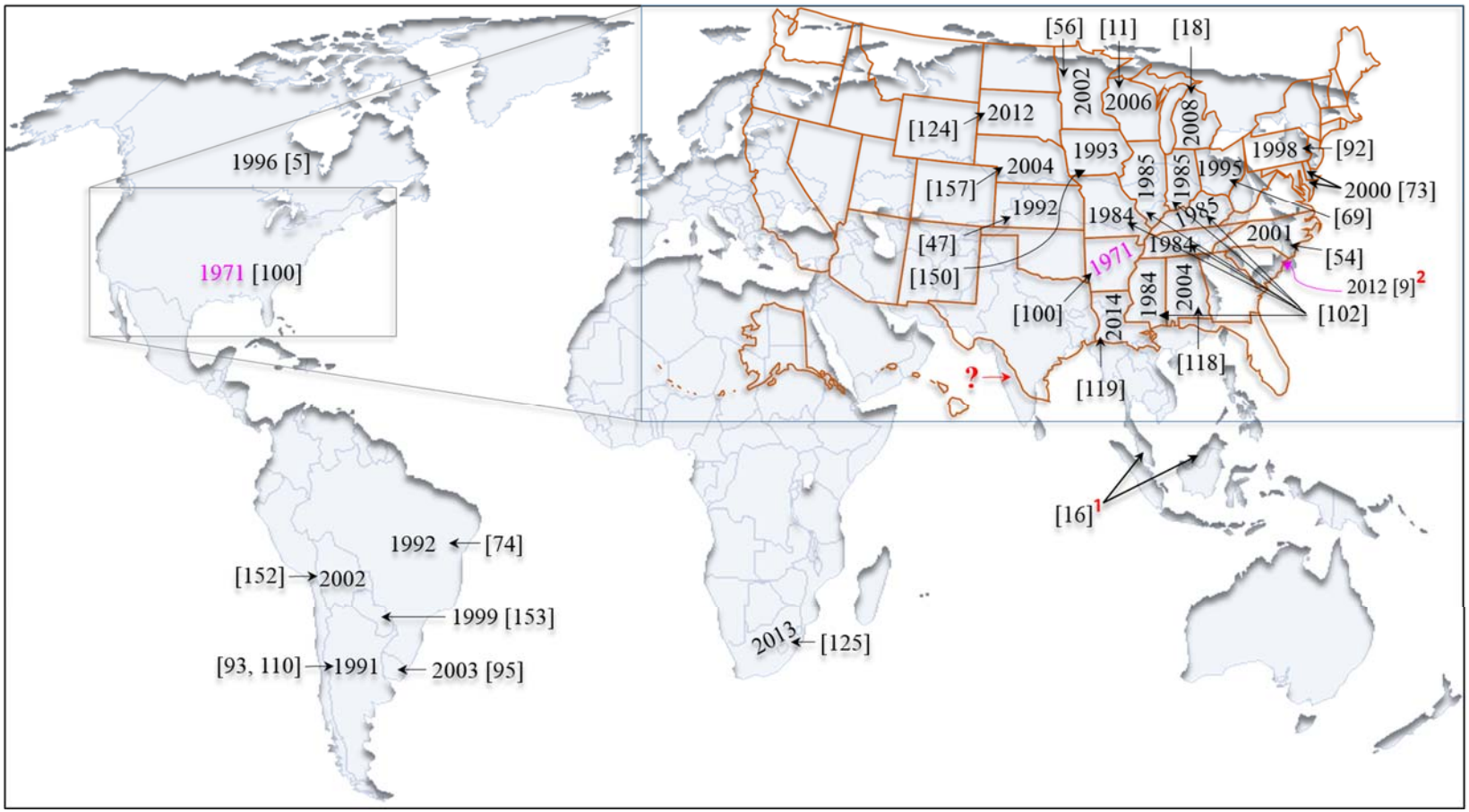

Figure 1: Distribution of soybean sudden death syndrome (SDS) pathogens with the year of first detection followed by citation. In North America, and South Africa *Fusarium virguliforme* and in South America *F. brasiliense*, *F. crassistipitatum*, *F. tucumaniae*, and *F. virguliforme*. [?]In India, *F. solani* f. sp. *glycines* reported not as SDS-causing pathogen but as a wilt causing pathogen in soybean; [1]In Malaysia, *F. virguliforme* isolated from soil but no reports of soybean SDS and [2]In Japan, *F. azukicola* has been reported inducing SDS symptoms on soybean.

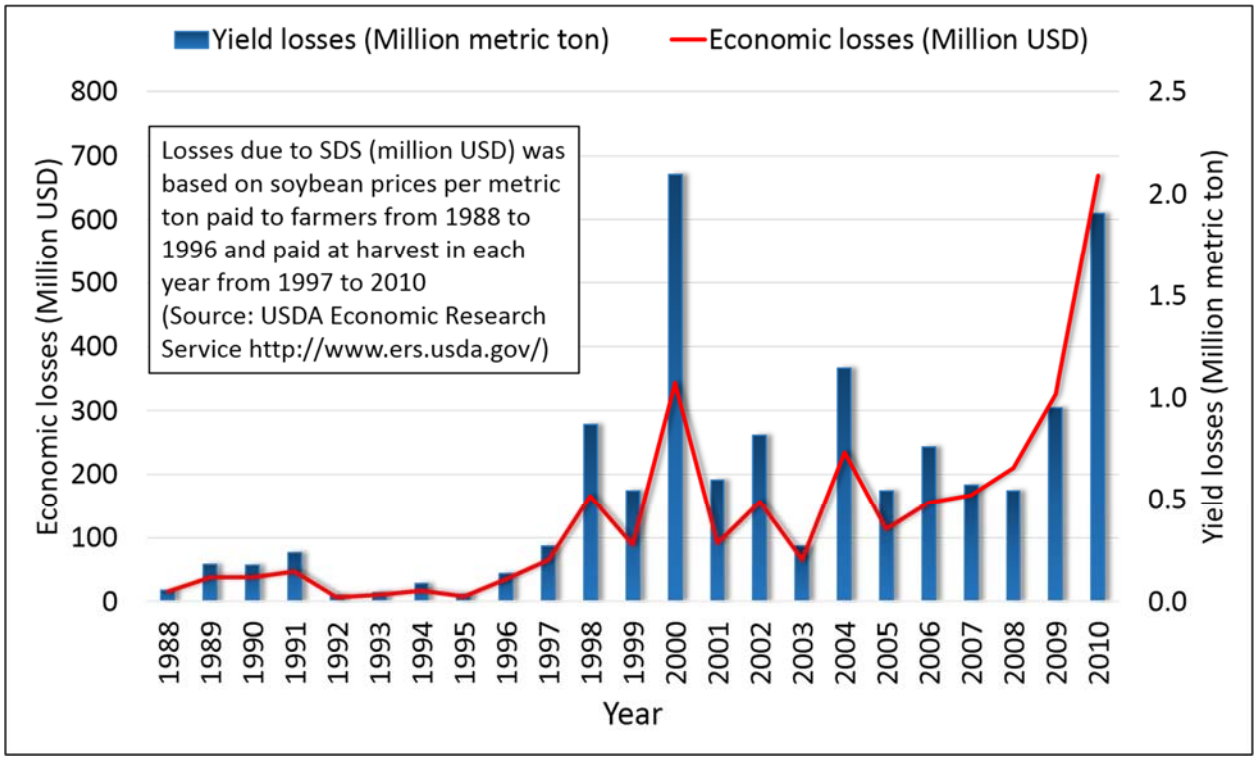

Figure 2: Yield and economic losses due to soybean sudden death syndrome (SDS) for the U.S.A. soybean production from 1988 to 2010. [Data source for yield loss: 21, 35, 53, 96, 116, 132–134, 136–141 and for soybean prices: USDA Economic Research Service www.ers.usda.gov/]

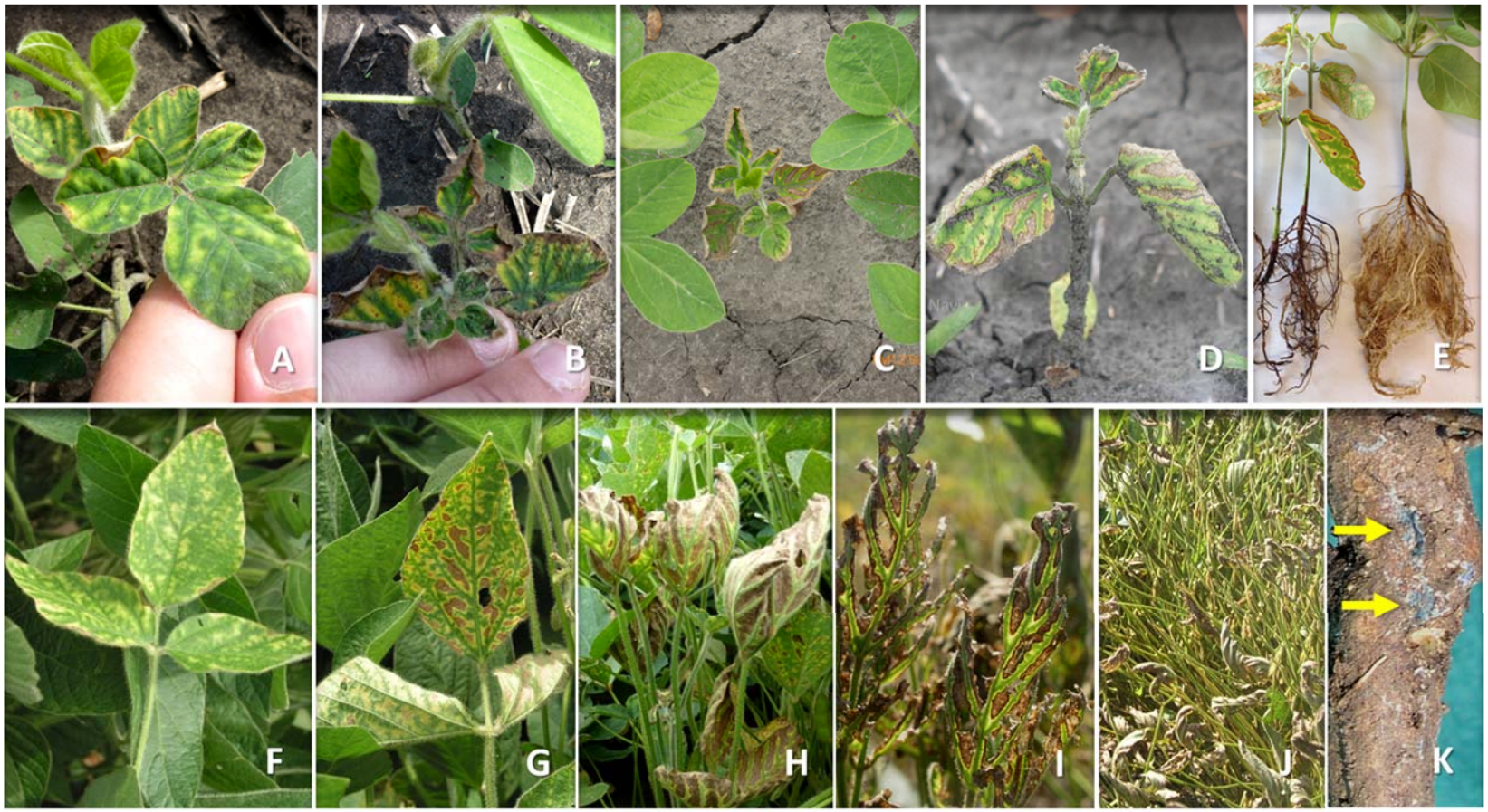

Figure 3: Field symptoms of soybean sudden death syndrome caused by *Fusarium virguliforme* in seedling stage; (A) chlorotic spots, (B) chlorosis, (C) stunting, (D) necrosis and puckering and (E) discolored basal stem, tap roots and root hairs of infected plants (left) and uninfected plant with healthy roots and leaves (right) and in reproductive growth stages; (F) chlorotic spots and chlorosis, (G) necrosis, (H) severe necrosis and puckering, (I) loss of leaf lamina (J) defoliation with leaf petioles intact on stems and (K) *F. virguliforme* growth on taproot.

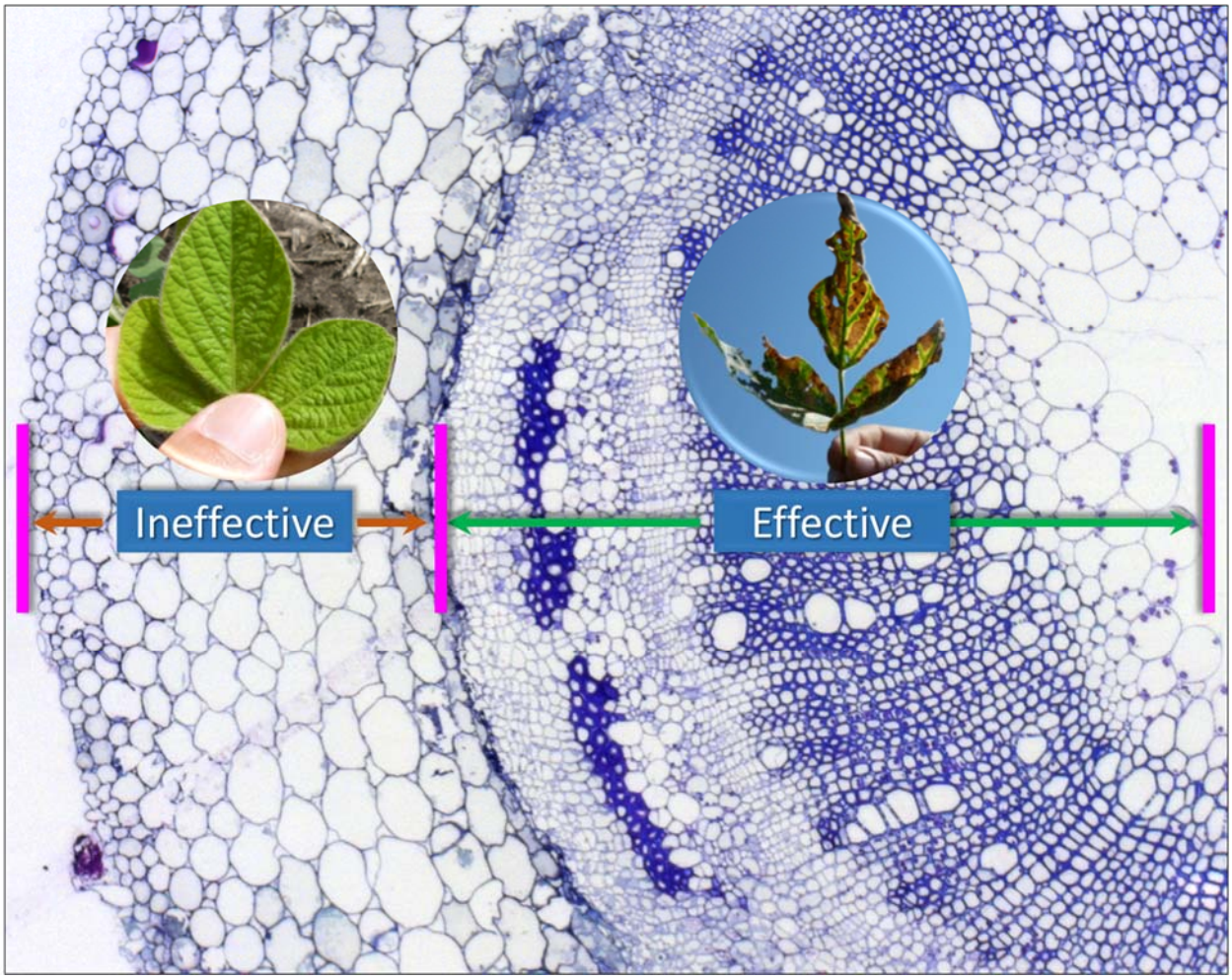

Figure 4: Effective and ineffective colonization zones of *Fusarium virguliforme* in the section of a soybean taproot [83].

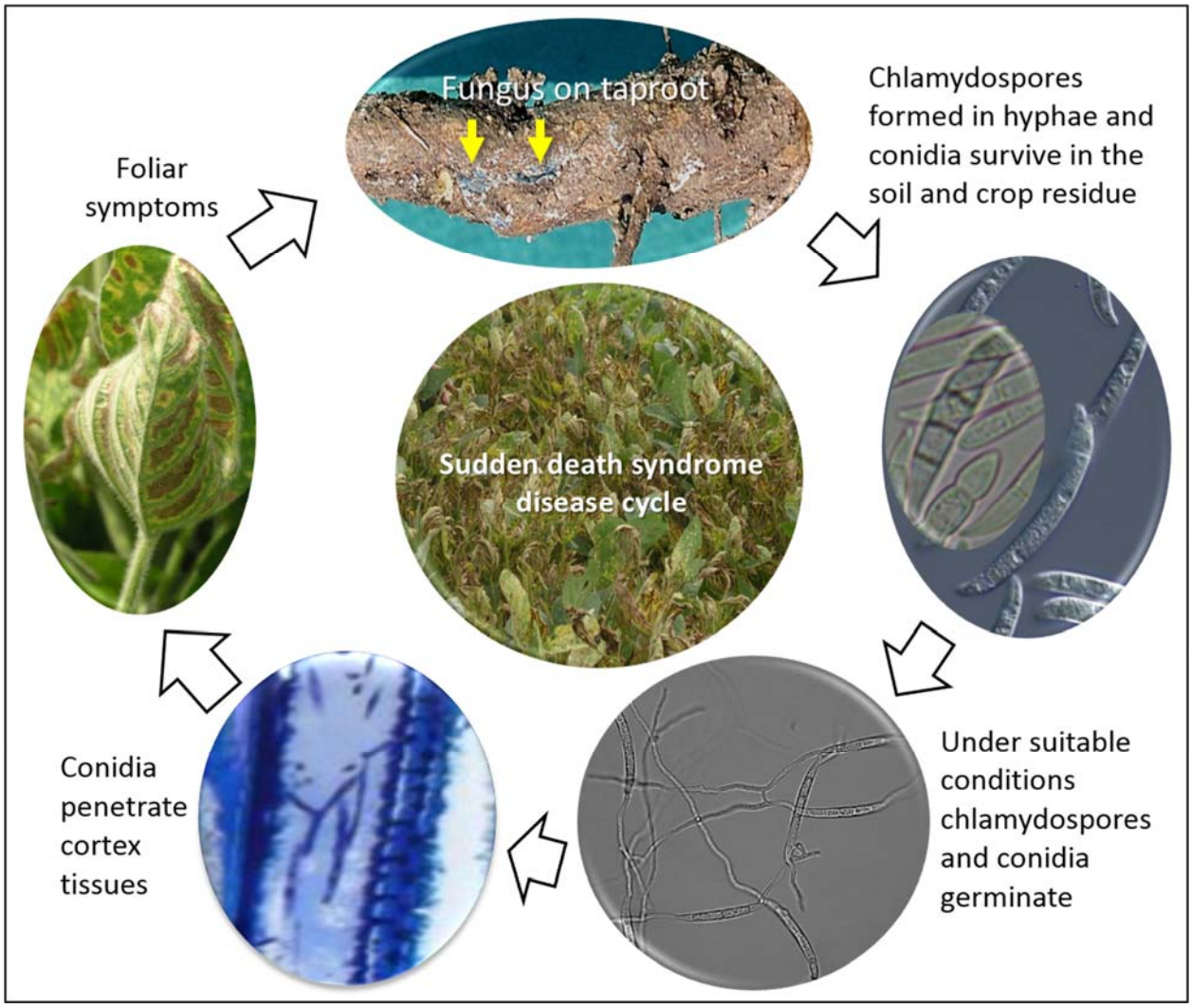

Figure 5: Disease cycle of sudden death syndrome of soybean caused by *Fusarium virguliforme.*

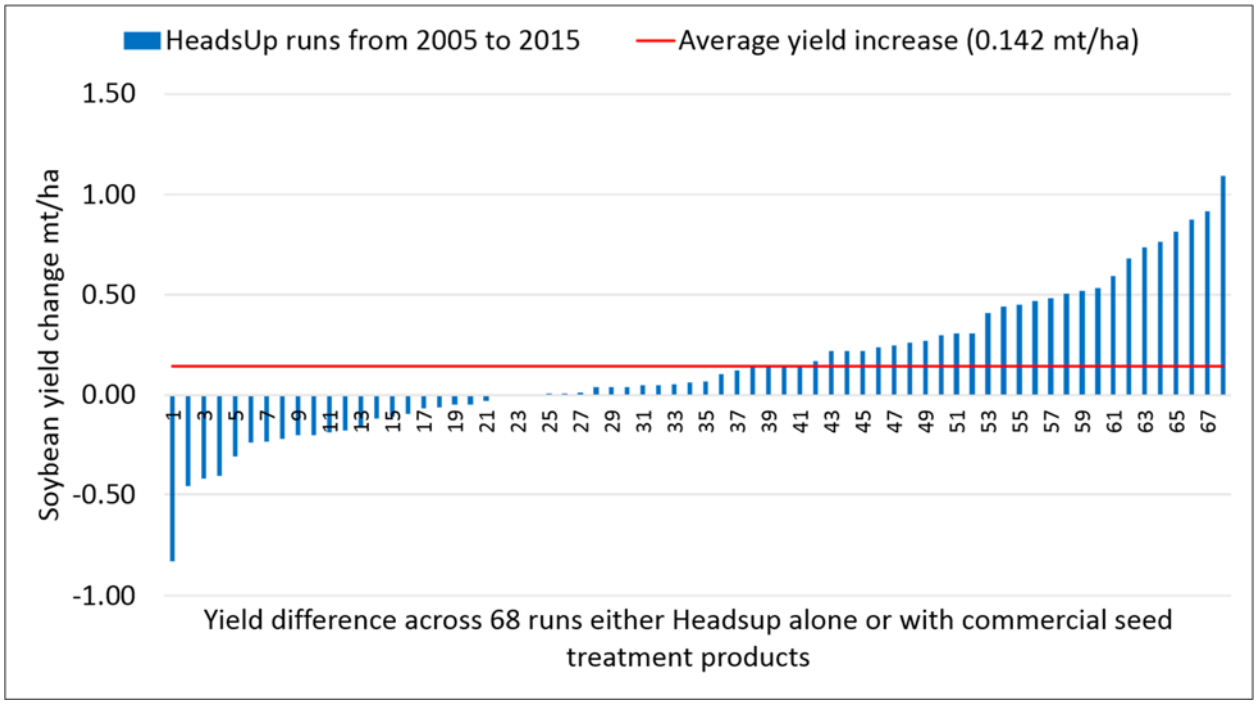

Figure 6: Effects of seed treatments with either HeadsUp alone or HeadsUp plus commercial seed treatment products on SDS reduction as indicated by yield increase. Trials were conducted in fields infested with SDS fungus in the U.S. Midwestern regions.

Figure 7: Greenhouse screening technique for: 1. efficacy tests of biocontrol agents or fungicides seed treatment and 2. identification of sources of resistance to soybean sudden death syndrome; (A) spread inoculum at 1% of the potting mixture in plastic tub, (B) Mix the inoculum with potting mixture, (C) Fill-up the cups, (D) Mark planting spots with hand held wooden planter (WP), (E) Place 5-7 seeds in marked spots and press the seed to uniform depth of 2-cm with WP, (F) Cover the seed with potting mixture and (G) Compact it with hand held wooden compactor (WC). Water twice daily to maintain enough moisture in cups, and F. Record stand counts and SDS counts 15, 30 and 45 days after planting.